POLLINATION ECOLOGY OF SEVEN SPECIES OF *BAUHINIA* L. (LEGUMINOSAE: CAESALPINIOIDEAE)[1]

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ABSTRACT

Pollination and floral biology of seven species of *Bauhinia* were analyzed between 1982 and 1983 in different Venezuelan plant communities. *Bauhinia* species are grouped in two sections: *Pauletia*, which includes trees, and *Tylotaea*, which includes lianas. The species of sect. *Pauletia* included in this study (*B. aculeata*, *B. multinervia*, *B. pauletia*, *B. ungulata*) have comparatively large, white flowers, while the species of sect. *Tylotaea* (*B. glabra*, *B. guianensis*, *B. rutilans*) exhibit different colors of flowers and variations in form and color of the upper petal. Nectar analyses were made for six *Bauhinia* species for sugar and amino acid composition. The species of sect. *Tylotaea* produce less nectar with a higher sugar concentration than those of sect. *Pauletia*. Hexose is dominant in species of sect. *Pauletia* except in *Bauhinia aculeata*, where sucrose is dominant. The species of sect. *Tylotaea* have comparatively small diurnal flowers and are visited by a great variety of bees, wasps, butterflies, and hummingbirds; those of sect. *Pauletia* are mainly nocturnal and bat-pollinated, but *Bauhinia aculeata* showed different behavior and could be intermediate between the two sections. The flower morphology, floral biology, pollinator species, nectar composition, and secretion tend to be associated with the life form of the two sections of *Bauhinia*.

In an ecological context, caesalpinioid legume flowers are less specialized than their mimosoid and papilionoid counterparts. Caesalpinioid flowers are open, usually with exposed pollen and nectar available to specialized and nonspecialized pollen vectors. Only in some of the advanced genera are resource conservation and pollinator selection evident (Arroyo, 1981). The Caesalpinioideae exhibit a great variety of pollinating agents and mechanisms with an entomophilous trend (Arroyo, 1981). For example, many *Cassia* species are bee-pollinated (Delgado et al., 1977). In this sense, ornithophily and chiropterophily are scarce (Arroyo, 1981).

Studies of chiropterophily have paid comparatively more attention to the legumes of the New World than of the Old World (Frankie & Baker, 1974; Heithaus et al., 1974, 1975; Howell, 1975; Bernhardt, 1982; Ramirez et al., 1984; Prance, 1985). Some neotropical *Bauhinia* species are bat-pollinated (Heithaus et al., 1974; Ramirez et al., 1984). However, Vogel (1954) reported that *Bauhinia galpinii* and *B. mucronata* are sphingophilous, and Arroyo (1981) suggested that many other species of *Bauhinia* are probably sphingophilous.

The flowers of neotropical *Bauhinia* species exhibit great diversity in form, size, and color, which has been poorly studied from an adaptive viewpoint. The species of *Bauhinia* are grouped in three sections according to Stuard da Fonseca Vaz (1979). Section *Pauletia* comprises trees and shrubs; in contrast, species of sects. *Tylotaea* and *Schnella* comprise climbing plants. For all *Bauhinia* species studied, the flowering periods occur during the dry season.

The following study provides information about the floral biology and pollinator activity of seven species of *Bauhinia* belonging to sects. *Pauletia* and *Tylotaea* found in different plant communities of Venezuela. The chemical composition, secretion, and volume of the nectars produced were analyzed for comparing both sections of *Bauhinia*.

DATES AND METHODS

Bauhinia is widely distributed in several ecosystems in Venezuela. The localities for this study

[1] We thank S. Tillet, W. S. Armbruster, S. Renner, P. Berry, A. Castillo, and P. Bernhardt for comments on the manuscript. We are also especially grateful to R. Wunderlin for help with plant identifications, and to F. Fernández Yepez, J. A. Clavijo, G. C. Eickwort, and O. Mielke for help with insect identifications. Special thanks are due H. Baker and I. Baker for the chemical nectar analyses. We extend gratitude to Y. Brito, A. Seres, N. G. Leal, C. Gil, M. López, L. Camero, H. Fariñas, and S. Gómez for assistance in the field.

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TABLE 1. Life form, reproductive phenology, and study sites of *Bauhinia* species.

Section Species	Life form	Flowering period	Fruiting period	Locality	Elevation (m)	Coordinate	Forest type[1]	Mean annual rainfall (mm)	Temperature (°C)
Pauletia									
B. aculeata	tree	Feb.-July	July-Nov.	Biological Reserve (Arboretum de la Escuela de Biología, Universidad Central de Venezuela), Colinas de Bello Monte, Caracas, Estado Miranda	1,100	10°30'N, 66°53'W	Dry Premontane Forest	550-1,100	18-24
				El Palmar village, 50 km NE of Upata, Estado Bolívar and 60 km of Imataca Forest Reserve	100	7°39'N, 66°07'W	Tropical Dry Forest	1,000-1,800	22-29
B. multinervia	tree	Nov.-Jan.	Dec.-Mar.	Along the Caracas River, Los Caracas, Distrito Federal, Departamento Vargas	8	10°37'N, 66°34'W	Dry Premontane Forest	550-1,100	18-24
B. pauletia	tree	Sep.-Nov.	Oct.-Mar.	San Sebastián de Los Reyes, Estado Aragua	200	9°56'N, 67°10'W	Dry Premontane Forest	550-1,100	18-24
B. ungulata	tree	Nov.-Jan.	Dec.-Mar.	Estación Biologica de Los Llanos, Sociedad Venezolana de Ciencias Naturales, approximately 12 km SE of Calabozo, Estado Guárico	75	8°56'N, 67°25'W	Tropical Dry Forest	1,000-1,800	22-29
Tylotaea									
B. glabra	liana	Sep.-Feb.	Oct.-May	Biological Reserve (Arboretum de la Escuela de Biología, Universidad Central de Venezuela), Colinas de Bello Monte, Caracas, Estado Miranda	1,100	10°30'N, 66°53'W	Dry Premontane Forest	550-1,100	18-24

TABLE 1. Continued.

Section Species	Life form	Flowering period	Fruiting period	Locality	Elevation (m)	Coordinate	Forest type[1]	Mean annual rainfall (mm)	Temperature (°C)
B. guianensis	liana	Feb.–Apr.	Mar.–May	Imataca Forest Reserve in the Estación Experimental de Río Grande, Distrito Piar y Roscío (Estado Bolívar), and Territorio Delta Amacuro	266	8°03'N, 61°39'W	Humid Tropical Forest	1,800	24
B. rutilans	liana	Sep.–Oct.	Oct.–Mar.	Henry Pittier National Park, close to Rancho Grande Biological Station, Estado Aragua	1,100	10°21'N, 67°41'W	Very Humid Premontane Forest	2,000–4,000	18

[1] According to Ewel et al. (1976).

were chosen in accordance with the flowering and fruiting periods indicated on specimens in the Herbario Nacional de Venezuela (VEN) and through field observations (Table 1) in various regions.

Field observations were made of the life form and height of plants, and pollination and floral biology were analyzed in 1982–1983 during the flowering and fruiting periods of each species.

FLORAL CHARACTERISTICS

The floral parts (corolla, pistil, stigma, and petal lengths) were measured using samples preserved in 70% ethanol for 20 flowers from five to ten individual plants of each *Bauhinia* species.

FLORAL BIOLOGY

Flowers were observed in situ to record anthesis: inflorescences with buds about to open were marked before anthesis, and progress of anthesis was observed every 30 minutes. The pattern of nectar production was measured periodically with microcapillaries inserted in the hypanthium cavity of bagged flowers. Solute concentration of the nectar was measured with a manual Bausch & Lomb refractometer (range 0–30%). The presence of sugar, proteins, amino acids, lipids, and other compounds was detected from nectar on filter paper by Drs. Irene & Herbert Baker (University of California, Berkeley, California, U.S.A.). Pollinator activity was observed and recorded during five days for each *Bauhinia* species. The visiting agents observed were captured with hand nets and mist nets and were examined for pollen load.

RESULTS

FLORAL MORPHOLOGY

The inflorescences of *Bauhinia* are axillary and/or terminal. The sect. *Pauletia* species have comparatively large, white flowers; the stamens are dimorphic: five are large and five short (Table 2). However, this trend was not clear for all species of this section. In *Bauhinia pauletia* short stamens are represented by five staminodes. The flowers of short and long pistils were found on the same tree of *B. aculeata*. The short pistil flowers are not located in the inflorescence. In 100 flowers of five individuals the large/short pistil ratio was 15 : 1. Floral dimorphism is associated with pistil length, with a significant difference between the two morphs ($t_{38} = 12.26$; $P < 0.0005$). The short pistils are associated with reduction of the gynophore ($\bar{X} = 1.12$, SD = 0.24 in large-pistil flowers and $\bar{X} = 0.54$, SD = 0.09 in short-pistil flowers), of style

TABLE 2. Measurements of different floral characteristics of seven *Bauhinia* species (in cm). (1) Inferior and lateral petals; (2) upper or principal petals; (3) staminodes; (4) short style; (5) from Ramirez et al. (1984).

		Flower				Stamen length		Pistil length			
Section Species	N	Length $\bar{X}$ (SD)	Width $\bar{X}$ (SD)	Color	Hypanthium $\bar{X}$ (SD)	Long $\bar{X}$ (SD)	Short $\bar{X}$ (SD)	Gynophore $\bar{X}$ (SD)	Ovary $\bar{X}$ (SD)	Style $\bar{X}$ (SD)	Stigma $\bar{X}$ (SD)
Pauletia (trees)											
B. aculeata	27	3.79 (0.30)	7.10 (0.39)	white (1, 2)	0.48 (0.11)	4.16 (0.25)	2.98 (0.22)	1.12 (0.24)	1.06 (0.09)	2.40 (0.20)	0.20 (0.00)
	13				0.42 (0.08)[4]	3.98 (0.31)	2.98 (0.19)	0.54 (0.09)	0.70 (0.10)	1.08 (0.18)	0.10 (0.00)
B. multinervia	5	10.53 (0.93)	9.78 (0.25)	white (1, 2)	3.04 (0.59)	7.28 (1.70)	6.10 (2.04)	4.50 (0.85)	2.34 (0.18)	3.92 (0.52)	0.78 (0.13)
B. pauletia	5	15.85 (1.14)	— —	white (1, 2)	1.20 (0.20)	7.20 (1.01)	2.87 (0.21)[3]	3.77 (0.76)	1.67 (0.15)	3.53 (0.29)	0.57 (0.15)
B. ungulata (5)	94	4.66 (0.65)	1.42 (0.22)	white (1, 2)	1.23 (0.17)	4.11 (0.39)	2.91 (0.45)	2.22 (0.46)	1.35 (0.32)	1.93 (0.65)	0.23 (0.07)
	20			red (3)	1.15 (0.14)[4]	4.12 (0.48)	2.80 (0.53)	1.60 (0.27)	1.12 (0.08)	1.12 (0.21)	0.18 (0.06)
Tylotaea (lianas)											
B. glabra	5	1.83 (0.45)	1.89 (0.42)	white (1) with purple lines (2)	— —	0.70 (0.00)	0.52 (0.05)	— —	0.34 (0.02)	0.29 (0.02)	0.05 (0.00)
B. guianensis	5	2.26 (0.03)	2.13 (0.02)	white (1) clear yellow (2)	— —	1.04 (0.05)	0.82 (0.08)	— —	0.43 (0.03)	0.36 (0.04)	0.05 (0.00)
B. rutilans	5	1.90 (0.20)	1.60 (0.28)	pink (1) yellow greenish (2)	— —	0.90 (0.07)	0.72 (0.08)	— —	0.43 (0.04)	0.30 (0.07)	0.05 (0.00)

($\bar{X}$ = 2.40, SD = 0.20; $\bar{X}$ = 1.08, SD = 0.18, respectively). The number of ovules per ovary is similar in both morphs but the ovules of short-pistil flowers are abortive. In *Bauhinia multinervia* there were no floral variations (Table 2).

The flowers of both sections are zygomorphic, the petals are different in form and size. In general, the inferior and lateral petals are similar in form, while their areas are slightly different (Table 3).

The flowers of sect. *Tylotaea* are smaller than those of sect. *Pauletia*; the average floral length varies from 1.83 to 2.26 cm. The gynophore and hypanthium are also shorter than in sect. *Pauletia*.

In *Bauhinia pauletia*, *B. multinervia*, and *B. ungulata*, one or two flowers open per night per inflorescence (Table 4). Anthesis, petal expansion, occurs at dusk between 1700 and 1900 hours, and the process is quick and synchronic (Fig. 1). *Bauhinia aculeata* has nocturnal anthesis but is comparatively asynchronous (2100–0300) and showed two peaks during anthesis (Fig. 1). In the species of sect. *Pauletia* anthers dehisce before anthesis.

In the species of sect. *Tylotaea* (lianas), anthesis is diurnal, occurring approximately between 0730 and 1130 hours. Petal expansion is slower, and the number of opened flowers per inflorescence per day is higher than in tree species of sect. *Pauletia* (Fig. 1). The pink flowers of *Bauhinia rutilans* showed two peaks during anthesis (Fig. 1). Although we did not record anthesis in *Bauhinia guianensis*, it occurs in the morning between 0900 and 1100 hours and is probably similar to that in *B. rutilans* (pers. obs.).

NECTAR SECRETION

In the arborescent *Bauhinia* species nectar is produced and accumulated in the hypanthium of flowers. Nectar production starts immediately after anthesis; however, in *B. multinervia* there was a little nectar before anthesis. The average volumes were high for *B. multinervia* (102.42 ml) and *P. pauletia* (47.32 ml); nectar concentration was relatively low and similar in the species studied (Table 5). The nectar of *B. aculeata* was produced during day and night; the average nocturnal production is significantly less than the diurnal production (t_6 = 8.55; $P < 0.0005$). This difference was associated with a diurnal floral activity higher than nocturnal. The solute concentration of nectar increased from the first hours after anthesis until midnight in *B. pauletia* and *B. multinervia*, while in *B. aculeata* the higher concentration of nectar occurred during the night period. The volume pro-

TABLE 3. Morphological characteristics of petals in six *Bauhinia* species. L = length, A = width.

Section Species	Inferior petals Area (cm^2)	L (cm)	A (cm)	L/A ratio	Form	Lateral petals Area (cm^2)	L (cm)	A (cm)	L/A ratio	Form	Upper petals Area (cm^2)	L (cm)	A (cm)	L/A ratio	Form
Pauletia (trees)															
B. aculeata	8.23	6.15	2.15	3 : 1	narrowly elliptic	8.07	6.10	2.12	3 : 1	narrowly elliptic	7.19	5.80	1.95	3 : 1	lanceolate
B. multinervia	11.43	10.55	1.60	3 : 1	lanceolate	10.21	9.70	1.45	3 : 1	lanceolate	7.92	8.90	1.40	6 : 1	very narrowly elliptic
B. pauletia	0.61	9.20	0.08	6 : 1	narrowly oblanceolate	0.66	9.60	0.08	6 : 1	narrowly oblanceolate	0.37	3.10	0.18	6 : 1	narrowly oblanceolate
Tylotaea (lianas)															
B. glabra	0.80	1.67	0.90	2 : 1	narrowly obovate	0.69	1.62	0.75	2 : 1	narrowly obovate	0.58	1.65	0.50	3 : 1	oblanceolate
B. guianensis	1.74	2.00	1.30	1.5 : 1	very elliptic	1.36	1.75	1.25	1.2 : 1	suborbiculate	0.58	1.80	0.40	6 : 1	very narrowly elliptic
B. rutilans	0.87	2.00	0.70	3 : 1	narrowly elliptic	0.84	1.95	0.65	3 : 1	narrowly elliptic	0.66	1.90	0.60	3 : 1	oblanceolate

TABLE 4. Floral biology and visiting agents of six species of *Bauhinia*. (1) = bats, (2) = birds, (3) = insects, (4) = with pollen load, (5) = not identified.

Section Species	Obser-vation hours	Anthesis hours	Number of opened flowers/inflorescences/day			Time of floral receptivity	Flower longevity	Visiting agents
			Range	$\bar{X}$	SD			
Pauletia								
B. aculeata	30	2100–0300	1–2	1.15	0.36	Nocturnal and diurnal	16 hr.	Apodiformes (2)
								Trochilidae
								Chrysolampis mosquitus
								Coleoptera (3)
								Scarabidae
								Leucothyreus sp. (4)
								Hymenoptera (3)
								Anthophoridae
								Xylocopa (Neoxylocopa) sp. (4)
								Xylocopa fimbriata Fab.
								Apidae
								Apis mellifera L. (4)
								Eulaema speciosa (Mocsary) (4)
								Lepidoptera (3)
								Hesperiidae
								Epargyreus sp. (4)
								Noctuidae
								(5)
								Pieridae
								Anteos clorindae Godart. (4)
								Aphrissa statica Cramer
								Eurema nise Cramer
								Ganyra menciae var. *janeta* (Dixey) (4)
								Sphingidae
								Eumorpha labruscae (L.) (4)
								Eumorpha vitis (L.) (4)
B. multinervia	29	1700–1830	1	1.00	0.00	Nocturnal	18 hr.	Chyroptera (1)
								Phyllostomatidae
								Phyllostomus discolor Wagner (4)
								Glossophaga soricina Pallas (4)

TABLE 4. Continued.

Section Species	Obser- vation hours	Anthesis hours	Number of opened flowers/ inflorescences/day Range	$\bar{X}$	SD	Time of floral receptivity	Flower longevity	Visiting agents
								Apodiformes (2)
								Trochilidae
								Phaethornis agusti
								Hymenoptera (3)
								Apidae
								Apis mellifera L. (4)
								Apis mellifera var. *scutellata* Lat. (4)
								Vespidae
								Synoeca surinama L.
								Lepidoptera (3)
								Hesperiidae
B. pauletia	17	1730–1900	1–2	1.05	0.21	Nocturnal	13 hr.	Chyroptera (1)
								Phyllostomatidae
								Phyllostomus discolor Wagner (4)
								Glossophaga soricina Pallas (4)
								Hymenoptera (3)
Tylotaea								
B. glabra	32	0530–0900	1–7	2.51	1.63	Diurnal	24 hr.	Hymenoptera (3)
								Anthophoridae
								Xylocopa (*Neoxylocopa*) sp. (4)
								Apidae
								Apis mellifera L. (4)
								Centris (C.) *aenea* Lepeletier (4)
								Trigona nr. *cupira* Smith (4)
								Formicidae
								Pseudomirmex sp. grupo *gracilis*
								Halictidae
								Pseudaugochloropsis sp. (4)
								Vespidae
								Polybia ignobilis (Holiday) (4)
								Lepidoptera (3)
								Hesperiidae

TABLE 4. Continued.

Section Species	Obser-vation hours	Anthesis hours	Number of opened flowers/inflorescences/day: Range	$\bar{X}$	SD	Time of floral receptivity	Flower longevity	Visiting agents
B. guianensis	12	0900–1100	—	—	—	Diurnal	9 hr.	Apodiformes (2) Trochilidae ? Hymenoptera (3) Apidae *Trigona williana* Friese (4) Anthophoridae *Gaesochira complanata* Moure & Michener (4) Halictidae *Megalopta* sp. (4) Vespidae *Polybia occidentalis* (4) *Synoeca surinama* L. (4) *Steiopolybia pallipes* Olivier Lepidoptera (3) Hesperiidae *Nastra insignis* (Ploetz)
B. rutilans	16	0430–1100	—	—	—	Diurnal	24 hr.	Apodiformes (2) Trochilidae *Schistes geoffroyi* L. Hymenoptera (3) Anthophoridae *Xylocopa* sp. (4) Apidae *Bombus* sp. (4) *Trigona fulviventris* Guerin Eumeminae (5) Vespidae *Stenodynerus* sp.

duced can exceed the volume of the hypanthium cavity, and without pollinating visits, nectar starts dripping down or out. *Bauhinia aculeata* produced nectar for 19 hours, whereas in *B. pauletia* and *B. multinervia*, production lasted approximately 13 hours. The secretion rate, estimated as the volume produced per time unit, was highest in *B. multinervia* ($\bar{X}$ = 7.88 ml/hr.), followed by *B. pauletia* ($\bar{X}$ = 3.61 ml/hr.) and *B. aculeata* ($\bar{X}$ = 0.27 ml/hr.). The first two species are characterized by nocturnal secretion. Significantly in *B. aculeata* no difference between diurnal (0.17 ml/hr.) and nocturnal (0.22 ml/hr.) secretion rates was found.

The species of sect. *Tylotaea* produced less volume of nectar with a higher sugar concentration than those of sect. *Pauletia* (Table 5). In *Bauhinia glabra* the volume was less than the minimal capacity of microcapillaries and only a sticky sap at the base of stamens and pistil was detected. In *B. rutilans* nectar secretion took place during seven hours and the rate was 0.27 ml/hr., similar to that in *B. aculeata* (sect. *Pauletia*), with a total of 1.88 ml per flower.

NECTAR COMPOSITION

The nectar of six *Bauhinia* species contained proteins, amino acids, phenols, and alkaloids, but no lipids were detected in the nectar of any of the species studied (Table 6). Alkaloids appeared in low quantities only in the nectars of *B. aculeata* and *B. rutilans*.

Only traces of protein were detected in the nectar of *B. multinervia* (sect. *Pauletia*), while in *B. glabra* and *B. rutilans* (sect. *Tylotaea*) it was detected in low quantities. The proportion of sugar in the nectar of sect. *Pauletia* showed that sucrose is dominant in *B. aculeata*, while *B. multinervia* and *B. ungulata* were hexose-dominant with similar proportions of glucose and fructose. The proportion of glucose was similar to sucrose in *B. glabra* but there was a higher proportion of both sugars than of fructose (Table 7).

There is a temporal change of the proportion of sucrose, glucose, and fructose in the nectars during the secretion period, with a decrease in the proportion of sucrose over time in the tree species. At the beginning of nectar secretion, the proportion of sucrose was 2.74 times higher than 12 hours later in *B. pauletia*, *B. multinervia* (both sect. *Pauletia*), and *B. rutilans* (sect. *Tylotaea*): when sucrose decreases, fructose and glucose increase in quantity and the sucrose/glucose + fructose ratio decreases (Table 7).

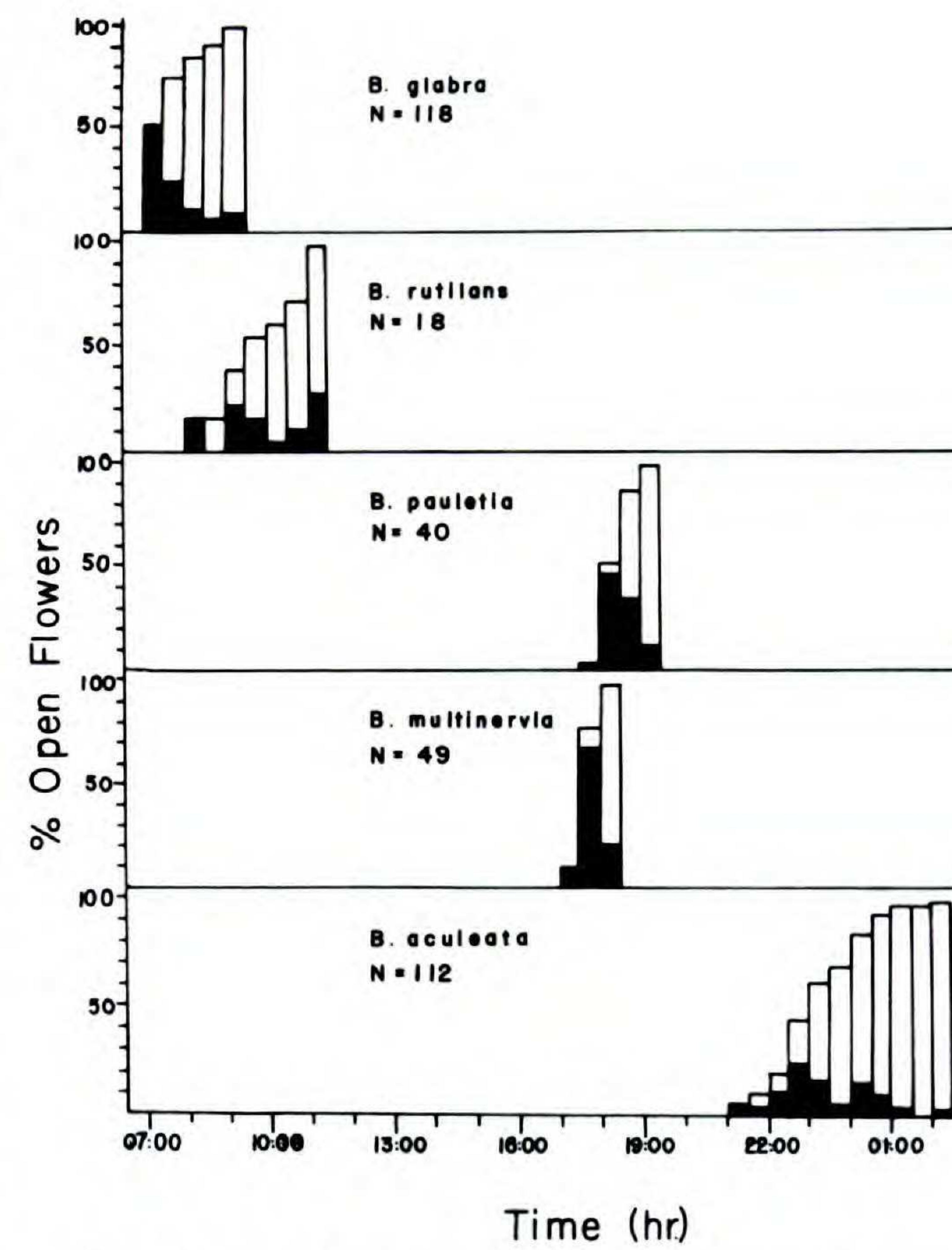

FIGURE 1. Anthesis expressed as the percentage of open flowers during half-hour intervals. □ % cumulative, ■ % non-cumulative.

The proportions of 20 amino acids analyzed differed in the nectar of different *Bauhinia* species, and varied from 3 to ≥ 10, using a relative scale (Table 6). The scale from 1 to 10 is based on standard concentrations of histidine. A value of 10 is equivalent to 3.9 mg histidine/ml, and each successive unit below 10 represents a halving of concentration (9 = 1.95 mg/ml; 8 = 0.975 mg/ml; and so forth) (Baker & Baker, 1975). The analyses showed that there was no difference in the presence of essential amino acids. Proline was dominant in all species except *B. multinervia*. Only one species studied, *B. rutilans*, had lysine in the nectar (Table 8).

POLLINATOR ACTIVITY

In bat-pollinated species of *Bauhinia* the flowers are exposed on the top of the foliage, and petals are separated, leaving the anthers exposed. The pollen adheres to the head and ventral part of the animal. The feeding activity and hence pollination last only seconds with the maximum occurring at dusk and in the first night hours. During the visit, *Phyllostomus discolor* and *Glossophaga soricina* seize the flowers and inflorescences so that the branches are bent down by the weight of the animal. Nocturnal visits were made by Sphingidae and but-

TABLE 5. Average volume and solute concentration of nectar for five *Bauhinia* species.

Section Species	Total volume of nectar (ml/flower)			Solute concentration (%)		
	Range	$\bar{X}$	SD	Range	$\bar{X}$	SD
Pauletia (trees)						
B. aculeata	3.96–5.81	5.03	0.95	12.0–28.0	19.35	4.85
B. multinervia	60.37–138.01	102.42	36.41	16.4–21.0	19.34	1.62
B. pauletia	14.18–87.44	47.32	37.12	13.0–18.0	16.23	2.07
Tylotaea (lianas)						
B. glabra	—	<0.24	—	—	≥30.00	—
B. rutilans	1.06–2.36	1.88	0.57	26.0–30.0	28.25	1.81

terflies, and phyllostomatid bats were observed on *B. multinervia* and *B. pauletia* flowers. *Phyllostomus discolor* and *Glossophaga soricina* bats were considered effective pollinators because they carried pollen on their heads and bodies (Table 4). During the day, the flowers of *B. multinervia* and *B. pauletia* were visited by butterflies, wasps, and hummingbirds, though there was little nectar and pollen. In addition, *B. multinervia* was visited between 0530 and 0800 hours by *Phaethornis aguti* (Trochilidae) to take nectar of open flowers from the previous night.

A different behavior was shown for *Bauhinia aculeata* (sect. *Pauletia*): during the night, flowers were visited by Sphingidae (*Eumorpha labruscae* and *E. vitis*) and infrequently by Noctuidae. Butterflies, wasps, bees, and hummingbirds were abundant during the day. The bees, *Xylocopa* (*Neoxylocopa*) sp., *Apis mellifera*, *Eulaema speciosa*, and several species of Pieridae (e.g., *Anteos clorindae*, *Ganyra menciae*) carried pollen of *B. aculeata*. These insects inserted their heads inside the flower and imbibed nectar. The hummingbird *Chrysolampis mosquitus* took nectar from the flower in the morning between 0600 and 0730 hours and at dusk between 1600 and 1830 hours.

The species of sect. *Tylotaea* have comparatively small flowers, which were visited by a great variety of bees, wasps, butterflies, and hummingbirds during the time of stigma receptivity (Table 4). *Bauhinia glabra* was visited by *Apis mellifera* and *Pseudaugochloropsis* sp. These insects arrived at the flowers posing on the inferior and lateral petals, introducing their body into the flower, while *Bombus* sp. inserts only its head into the flower. The most frequent visits were by *A. mellifera* and *Bombus* sp. during the morning.

Bauhinia guianensis was visited by *Xylocopa* sp. and *Synoeca surinama* in the morning and afternoon. These bees carried pollen on the legs and head. A species of butterflies (*Nastra insignis*, Hesperiidae) took nectar about noon, but it was not a pollinator. In addition, one unidentified hummingbird was observed for a long time visiting the flowers. *Bauhinia rutilans* was visited by bees, wasps, and hummingbirds; *Xylocopa* sp. and *Bom-*

TABLE 6. Proportion of organic compounds in nectar of six *Bauhinia* species (arrows indicate temporary trends after anthesis).

Section Species	Amino acids[1]	Phenols	Alkaloids	Proteins
Pauletia (trees)				
B. aculeata	6	tr	slightly+	ND
B. multinervia	5 → ≥10*	± → ++	ND	tr
B. pauletia	3 → 7	tr → +	ND	ND
B. ungulata	6	tr	ND	ND
Tylotaea (lianas)				
B. glabra	6 → >10	+	ND	tr
B. rutilans	3 → 7	+ → ++	slightly+	+

tr = traces; * = suggests breakdown during the night; ND = not detected; [1] = scale from 1 to 10 of relative quantities; + = moderate; ++ = abundant.

TABLE 7. Proportion of nectar sugars and their temporal variation (variations in time are in the direction of the arrows after anthesis).

Section Species	Proportion of sugars					Sucrose/ glucose + fructose
	Melezitose	Maltose	Sucrose	Glucose	Fructose	
Pauletia (trees)						
B. aculeata	—	—	0.552	0.241	0.208	1.279[a]
B. multinervia	0.005 → 0.111	—	0.167 ← 0.211	0.329 → 0.446	0.368 → 0.460	0.203 ← 0.413[b]
B. pauletia	—	—	0.188 ← 0.516	0.279 → 0.463	0.206 → 0.349	0.246 ← 0.153[b]
B. ungulata	0.016	0.006	0.185	0.443	0.350	0.233[b]
Tylotaea (lianas)						
B. glabra	0.007	—	0.330	0.388	0.274	0.499[c]
B. rutilans	—	—	0.365 ← 0.558	0.234 → 0.369	0.208 → 0.224	0.573 ← 1.261[a]

[a] sucrose dominant, [b] hexose dominant, [c] intermediate between a and b.

bus sp. were abundant collecting pollen during the middle of the day. The flowers were visited frequently by *Schistis geoffroyi* (Trochilidae) and the pollen was collected on their bills. In addition, the flowers were perforated externally at the base by an unidentified nectar-robbing species of hummingbird.

DISCUSSION

The morphology, color, and scent of flowers are associated with size and behavior of pollinators. Chiropterophilous flowers are often white, exposed above the foliage, nectar continuously, show nocturnal anthesis, and have a disagreeable smell (e.g., Heithaus et al., 1974; Sazima & Sazima, 1975, 1978; Voss et al., 1980; Howell & Schropfer Roth, 1981; Ramirez et al., 1984). Entomophilous species, including those of *Bauhinia*, have flowers of smaller size, of varied color, fragance, diurnal anthesis, and low nectar production. In addition, bee flowers often have dense inflorescences (e.g., Bolten & Feinsinger, 1978; Frankie et al., 1983). Such floral characteristics as flower size and time of anthesis of the studied *Bauhinia* species can be related to their different pollination systems. The white-flowered *Bauhinia pauletia* and *B. multinervia* are chiropterophilous, and *B. glabra* and *B. guianensis* are entomophilous, while the pink flowers with red bracts of *B. rutilans* were visited frequently by hummingbirds, which carry pollen.

In most chiropterophilous species, anthesis seems to occur at dusk (1800–2000 hours) (Heithaus et al., 1974; Sazima & Sazima, 1975; Gould, 1978; Lack, 1978; Ramirez et al., 1984). Anthesis of *Bauhinia pauletia* and *B. multinervia* occurred at similar evening hours. The flowers last one night, similar to *Markea neurantha* (Solanaceae) (Voss et al., 1980), *Lafoensia pacari* (Lythraceae) (Sazima & Sazima, 1975), and *Bauhinia ungulata* (Ramirez et al., 1984). In *Passiflora mucronata* (Passifloraceae) anthesis occurs between 0100 and 0200 hours, with a duration of less than 12 hours (Sazima & Sazima, 1978). The nocturnal flowers of *Bauhinia* can be considered as synchronic in anthesis because more than 50% of the flowers open within 30 minutes. The total process occurs in two and one-half hours. Anthesis of *Bauhinia glabra* and *B. rutilans* is diurnal, unimodal, and asynchronous, the peak of flower opening involving less than 40% of the flowers.

In *Bauhinia aculeata*, anthesis is nocturnal and asynchronous, with two peaks of less than 40% each; this asynchronic anthesis could promote cross-fertilization; the flowers are visited by a variety of pollinators. *Bauhinia aculeata* showed a combination of floral features: the floral morphology, nectar chemistry, timing of anthesis, and the pattern of nectar production cannot be placed with the other species studied. *Bauhinia aculeata* could be intermediate between nocturnal and diurnal pollination because a great number of specialized and unspecialized diurnal and nocturnal floral visitors and pollinators are associated with this species.

In bat-pollinated plants, higher production of nectar has been reported than in hummingbird- and butterfly-pollinated plants, and nectar production is continuous (Cruden, 1976; Baker, 1978). Nectar production in *Bauhinia pauletia* and *B. multinervia* is higher than in *Ochroma*, *Parkia*, *Chiranthodendron*, and *Lafoensia pacari*, which produce 5 to 20 ml/flower or inflorescence (Heithaus et al., 1975; Sazima & Sazima, 1975; Voss et al., 1980).

Flowers visited by bees frequently produce low nectar quantities. Frankie et al. (1983) found dif-

TABLE 8. Amino acid composition in nectar of six species of *Bauhinia*.

Section Species	Amino acids												
	Ala*	Argo	Asp	Aspt	Cys	Glu	Glut	Gly*	Histo	Isolo	Leuo	Lyso	Meto
Pauletia (trees)													
B. aculeata	+	+	+	?	+	+	+	+	±	+	+	ND	+
B. multinervia	+	±	+	?	+	+	+	+	±	+	±	ND	+
B. pauletia	+	+	++	+	+	+	+	+	?	+	+	ND	+
B. ungulata	+	±	+	ND	+	+	+	+	ND	ND	ND	ND	+
Tylotaea (lianas)													
B. glabra	±	+	+	+	+	+	+	+	ND	?	?	ND	+
B. rutilans	+	+	tr	ND	ND	+	ND	+	ND	tr	tr	+	?

o = essential amino acids for insect nutrition
* = amino acids in nectar of hummingbird-pollinated plants
tr = traces
ND = not detected
++ = strong
+ = good
± = moderate

ferent flower sizes associated with the daily nectar production. These authors defined moderate nectar production as 1.0 to 8.0 μl/day and high nectar production as on average higher than 8.0 μl/day. In addition, bee plants with elevated concentrations of solutes have small flowers and low nectar production (Hainsworth & Wolf, 1972; Baker, 1975). However, *Bauhinia glabra* and *B. rutilans* differ from this expectation since they produce higher volumes of nectar than those reported by Frankie et al. (1983). In addition, the visits and pollen load on *Schistis geoffroyi* (Trochilidae) suggest the importance of birds in the pollination systems of *B. rutilans* at the canopy level, so this species cannot be considered as a strictly melitophilous species.

The solute concentration of bat-pollinated flowers is frequently low (Howell, 1975, 1978; Baker, 1978; Steiner, 1983), and an increase of solutes from early to later hours after anthesis has been reported, e.g., in *Lafoensia pacari* from 6.8% to 11.0% (Sazima & Sazima, 1975). By contrast, Ramirez et al. (1984) showed in *Bauhinia ungulata* a higher solute concentration immediately before anthesis, which then decreased from 15.4% to 12.0%.

Percival (1965) found an increase in solute concentration with flower age in species of sect. *Tylotaea* and *B. aculeata* (sect. *Pauletia*). The increase in nectar concentration can increase the exploitation efficiency in flowers with low quantities of nectar (Hainsworth & Wolf, 1976). The nectar concentration of *Bauhinia multinervia* and *B. pauletia* flowers decreased with flower age. In the chiropterophilous species the visits are probably more frequent at the first hours after anthesis. In contrast, nectar concentrations of melitophilous-ornithophilous species (*B. glabra* and *B. rutilans*, respectively) increased at the midday hours. The increase of nectar concentrations and the higher pollination activities could be related to the temperature elevation during midday hours and concomitant evaporation from the nectar. Bees and hummingbirds prefer nectar up to 20% or 40% of sugar concentration (Percival, 1974; Baker, 1975).

The flowers of sect. *Pauletia* produce nectar during approximately 12 hours. Heithaus et al. (1974) reported a rate of nectar secretion of 0.5 ml/hr. for the first hours of production (from 1800 to 2300) in *B. pauletia*; however, the total rate of nectar secretion was 3.16 ml/hr. *Bauhinia pauletia* and *B. multinervia* showed a higher rate than *B. ungulata* (Ramirez et al., 1984). The difference could be associated with the greater flower and hypanthium cavity sizes of the first two species.

Nectar has a variety of nutritional compounds (Percival, 1965) and elements with a selective function (Baker & Baker, 1975). The alkaloids in *Bauhinia aculeata* (sect. *Pauletia*) and *B. rutilans* (sect. *Tylotaea*) probably reflect a selective force at pollination level. The high diversity of visiting agent species in both plant species could be selected by deterrent compounds. The absence of nectar proteins in the species of sect. *Pauletia* is related to bat pollination because some pollinating bat species eat insects (Heithaus et al., 1975) and pollen as a protein source (Alvarez & Quintero, 1969; Howell, 1974). In contrast, the nectars of

TABLE 8. Continued.

Amino acids						
Phe°	Pro*	Ser*	Tyr	Treo°	Trip°	Val°
+	++	+	+	+	±	+
+	+	+	?	+	+	+
±	±	+	±	+	+	+
+	++	+	ND	+	ND	±
+	++	+	+	+	?	+
ND	tr	tr	ND	tr	+	+

the species of sect. *Tylotaea* have some proteins; the insects that visit these species presumably obtain their nitrogenous requirement mainly from nectar and pollen, while hummingbirds obtain their nitrogenous requirement from nectar.

Flowers pollinated by butterflies and hummingbirds are reported as rich in sucrose, while nectar of bat flowers tends to be rich in hexose (Baker, 1978), and the nectar of bee flowers has no definite pattern in sugar proportions. *Bauhinia multinervia*, *B. pauletia*, and *B. ungulata* are hexose-dominant chiropterophilous species and have nocturnal nectar secretion. In these species, sucrose decreases with time, and glucose and fructose increase simultaneously. This pattern suggests a breakdown of sucrose, and then the sucrose/glucose + fructose ratios decrease. The breakdown of sucrose can be considered an advantage for pollination because bats cannot assimilate sucrose (Harborne, 1977). This pattern has been found in *B. rutilans* but was associated with hummingbird and bee pollination. *Bauhinia glabra* is rich in sucrose and glucose and has an entomophilous pollination system.

The flower morphology, floral biology, pollinator species, nectar composition, and timing and amount of secretion are associated with life form and subgeneric designation of the *Bauhinia* species studied. The species of sect. *Pauletia* are trees or shrubs, frequently pollinated by bats. In contrast, the species of sect. *Tylotaea* are lianas, pollinated by insects and birds. The pollinator specificity among *Bauhinia* species with similar pollinators is achieved basically through their geographic distributions. Sympatric distribution and overlapping flowering periods were found only for *Bauhinia* species of different sections. In this sense, the most important attribute is floral morphology. The floral characteristics and pollination biology provide additional characters for *Bauhinia* systematics. The agreement among reproductive and taxonomic properties could be related to evolutionary patterns at the sectional level.

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